CYTOGEOGRAPHY OF SEDUM LANCEOLATUM AND ITS RELATIVES

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Some species of *Sedum* that are widely distributed in the United States have two or more chromosome races. In several species these races differ by simple polyploidy, e.g., n = 8, 16 and 24 in *S. ternatum* Michx. (Baldwin, 1943; Uhl, 1970); n = 12, 24, 36 and 48 in *S. wrightii* A. Gray (Uhl, 1972). In other species the chromosome races differ in other species n = 14 and 22 in

the chromosome races differ in other ways, e.g., n = 14 and 22 in S. glaucophyllum Clausen (Uhl, 1970); n = 14, 15 and 16 in S. cockerellii Britton (Uhl, 1972). Two patterns of numerical variation have been described (Uhl, 1972): one, called "casual variation," in which occasional plants (usually trisomics and plants with B-chromosomes) differ from others of the same population, and the other, called "established variation," in which plants of some populations consistently differ from plants of other populations in their chromosome numbers. Presumably, established variants originated as casual variants whose karyotypes became fixed in their populations.

This paper is part of a general survey of the cytotaxonomy of the Crassulaceae in the United States and Mexico. It reports the chromosome numbers of about 320 collections, representing a broad geographical sample, of nine yellow-flowered species of Sedum that are native to the western United States and Canada. The classification follows Clausen (1975), who has made a detailed taxonomic study of all of these species and has published chromosome counts of about 40 collections, including a dozen of those reported here. In eight of the species the basic karyotype clearly consists of 8 chromosomes that are rather large compared to those of most other species of Sedum, and these species are considered to represent a single natural group (Clausen, 1975). The ninth species, S. oreganum Nuttall (n = 12), seems relatively isolated both cytologically and taxonomically. The data allow some observations regarding the probable role of polyploidy in evolution of these species.

Collections were made and studied sporadically over a period of more than 20 mode D l and Studied Sporadically over a period

of more than 20 years. Buds were fixed in modified Carnoy's solution (3 parts chloroform, 2 parts absolute ethanol, 1 part

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glacial acetic acid) sometimes directly from plants in the wild, more often from field-collected plants in cultivation. A few seemingly discrepant counts should probably be checked, since it is possible, despite all precautions, that rodents or sparrows might have mixed some plants cultivated in the cold frame. Anthers were squashed in acetocarmine, the chromosomes were studied at meiosis in pollen-mother cells, and the slides were made permanent. Most herbarium vouchers are in the Wiegand Herbarium or the Bailey Hortorium of Cornell University; some are at the University of California, Berkeley, where part of this study was conducted. Thanks are extended to the many persons who contributed collections and expecially to Mrs. Margaret Evans of Reno, Nevada, who provided a number of collections from remote localities.

Collections studied are listed in Appendix 1, arranged approximately from north to south and from west to east. Except as indicated by asterisks, only one plant of a collection was studied.

Sedum lanceolatum Torrey is listed as S. stenopetalum Pursh in many floras (see Clausen, 1948). It is by far the most widely distributed of the species, ranging from Alaska to the Black Hills of South Dakota and south to the southern Sierra Nevada of California, northern Arizona and New Mexico. It is most often found on granitic rocks and on their outwash, and it appears to be scarce, or probably absent, from lavas and basalt, as in the southern part of the Cascade Range and on the Columbia Plateau. Diploids (n = 8), tetraploids (n = 16) and hexaploids (n = 24)occur, mostly or entirely as established variants. Each level of ploidy is widespread (Figure 1) and exhibits considerable morphological diversity. No obvious morphological characters allow plants with one level of ploidy to be consistently distinguished from those with the others. It seems likely that polyploidy has evolved within the species more than once. Diploid Sedum lanceolatum (n = 8, Figure 2) was found at 71 localities: in the eastern Canadian Rockies, in Glacier Park, in the Uinta Mountains of Utah, in the Front Range of the Colorado Rockies, on summits in the Klamath Mountains of southwestern Orgeon and northwestern California, and scattered elsewhere. In elevation it ranges from alpine tundra above

3700 meters (e.g., Trail Ridge in Rocky Mountain National Park) down to the level of the western Great Plains (e.g., vicinity



Figure 1. Distribution of diploid (squares), tetraploid (circles) and hexaploid (triangles) plants of *Sedum lanceolatum* in the western United States and Canada. In some areas all collections are not indicated.

of Boulder and Denver, Colorado) and still lower farther north. Three casual variants were found: one apparent trisomic, a polysomic (Figure 3, see below) and one plant with a small Bchromosome (Figure 4).

Tetraploid Sedum lanceolatum (n = 16, Figure 5) was found at 107 localities: in the Black Hills of South Dakota, in the Bighorn, Beartooth, Medicine Bow, and Sherman Mountains, and in the eastern part of Yellowstone Park, all in Wyoming, in most of Colorado west of the crest of the Front Range, in



Figures 2-17. Chromosomes of Sedum at metaphase I in pollen-mother cells. *2000. 2-7, S. lanceolatum: 2, U400, n = 8; 3, U2208A, n = 9 + 1 (arrow indicates univalent; one bivalent is not in good focus); 4, U1954, n = 8 + 1B; 5, U405, n = 16; 6, U1715, n = 16 + 1B; 7, U974, n = 24. 8, S. debile, U1059, n = 8. 9, S. divergens, U1183, n = 8. 10, S. leibergii, U1035, n = 8. 11, S. radiatum ssp. radiatum, U903, n = 8. 12, S. radiatum ssp. ciliosum, U944, n = 8. 13, S. radiatum ssp. depauperatum, UC62.1115, n = 8. 14, S. rupicolum, U1040, n = 16. 15, S. stenopetalum, U1046, n = 32. 16, S. oreganum, U383, n = 12. 17, S. borschii, C42-31, pentaploid, with 16 bivalents and trivalents (most of them having a more "solid" appearance here because of their greater depth of focus) and 4 univalents, indicated by lines, around the

edges of the plate.

eastern Oregon, in northern Arizona and New Mexico, and scattered elsewhere. It occurs in alpine tundra in the Beartooth Mountains of northwestern Wyoming and at several places in Colorado (e.g., Loveland Pass, 3650 meters). It is also abundant at lower elevations with sagebrush on gravelly outwash deposits in Middle Park (Grand County, Colorado) and elsewhere. Two casual variants, one probable trisomic and another with a large B-chromosome (Figure 6), were found.

Hexaploid Sedum lanceolatum (n = 24, Figure 7) was found at 40 localities: in the Sierra Nevada of California, on several isolated ranges in Nevada, in southwestern Utah (Zion Park), at sea level around northern Puget Sound and adjacent waters, in the Okanogan Valley and Wenatchee Mountains of south central British Columbia south to central Washington, in western Yellowstone Park and the Grand Tetons, and in a small area of the Gore Range in central Colorado. On the basis of herbarium records, the species appears to be common in the high Sierra Nevada, and hexaploids probably occur there above timberline. Clearly, each level of ploidy is represented at a wide range of elevations, and no relationship of ploidy to elevation is detectable. Clausen's (1975) reports of counts from 10 other scattered localities mostly conform to the distributions of the chromosome races found in the much larger sample reported here. Some areas appear to have only one chromosome race of Sedum lanceolatum, but others have more. Only diploids were found in the eastern Canadian Rockies (4 localities) south through the vicinity of Glacier Park, Montana (6 localities). The northern part of the Front Range in Colorado to south of Denver seems to be populated only by diploids from the crest eastward (35 localities), but tetraploids are found just west of the crest and also just south of Pikes Peak. To the north, the eroded Sherman Mountains (southern Laramie Mountains) also have diploids in the east (5 localities), and tetraploids to the west (6 localities). Although some samples are small, the Uinta Mountains appear to be populated only by diploids (4 localities), the Black Hills (13 localities, including 9 collections of Professor R. T. Clausen not listed in Appendix 1) and Medicine Bow Mountains (6 localities) appear to have only tetraploids, and

the Grand Tetons (3 localities) and Sierra Nevada (3 localities)

only hexaploids. Samples from other mountain ranges are either too small or mixed in their ploidy.

In several areas, collections of different levels of ploidy were made within short distances of one another. However, most of these cases seem to correspond to boundaries between chromosome races, and it is not clear how much mixing, if any, occurs within the same population. Southeast of Vail Pass in central Colorado a tetraploid (U2276) was found less than a kilometer from a hexaploid (U1710). Six other hexaploid collections were made within about 16 km. of this locality, and the nearest other tetraploid came from about 10 km. away. From the Fall River road in Rocky Mountain National Park, a plant was found (U2208A), along with two normal diploids (U2208B, U2208C), which formed 9 bivalents and a univalent at metaphase I (Figure 3). Presumably this polysomic plant descended from a diploidtetraploid hybrid. The nearest known locality for a tetraploid is at Milner Pass, about 10 km. west. All three chromosome races of Sedum lanceolatum occur in Yellowstone Park. In the eastern part of the park 12 collections in the valley of the Yellowstone River and its tributaries were tetraploid, and two were diploid. In the western part 13 hexaploid collections came from Mammoth Hot Springs south into the valley of the Madison River and its tributaries, along with one tetraploid and one diploid. Plants collected in 1969 and 1973 from rocks on the hill overlooking Old Faithful were hexaploid, whereas on decomposing geyserite near Giantess Geyser, less than 400 meters to the west, the collection (U1052) was diploid. In the Big Horn Mountains of Wyoming, 15 collections were tetraploid, with a single diploid found in Tensleep Canyon about 6 km. below the nearest tetraploid. In the Little Belt Mountains of central Montana a collection at Kings Hill Pass was tetraploid, but another collection 10 km. north was diploid. Some other scattered cases of different levels of ploidy were found in nearby collections, and doubtless further study would reveal more. Clausen (1975) recognized three subspecies of Sedum lanceolatum, chiefly on the basis of plant size. The largest, subsp. nesioticum (G. N. Jones) Clausen, occurs near sea level in the vicinity of Puget Sound and the Strait of Georgia, and both

populations studied were hexaploid (n = 24). The diminutive subsp. subalpinum (Blankinship) Clausen is adapted to the brief

growing season of timberline and above. However, it intergrades with the larger subsp. lanceolatum, and Clausen (1975, p. 231) considered it "at an evolutionary stage somewhere between ecotype and subspecies." These two subspecies are not distinct cytologically and are listed together in Appendix 1. On Trail Ridge in Rocky Mountain National Park diminutive plants near timberline are diploid (n = 8), but in the Beartooth Mountains, northeast of Yellowstone Park, similar plants are tetraploid. Most collections clearly belong to the wide-ranging, intermediate-sized subsp. lanceolatum, which includes diploids, tetraploids and hexaploids. The type collection of Sedum lanceolatum was made by Dr. E. P. James, an army surgeon who was also botanist and geologist for the expedition to the Rocky Mountains led by Major Stephen H. Long in 1820 (Torrey, 1828). During two weeks in July of that year the expedition explored the eastern base of the Front Range, roughly from the present sites of Denver to Pueblo, Colorado (Fuller & Hafen, 1957). On July 13 and 14, James and two companions made the first recorded ascent of Pikes Peak, collecting plants along the way and traversing a region just below timberline where ". . . the yellow flowered stone-crop (Sedum stenopetalum, Ph.) [surely S. lanceolatum] is almost the only herbaceous plant which occurs" (James, 1823, vol. II: 26-27). Although no plants from Pikes Peak itself have been studied cytologically, two collections from 7 and 11 km. south of its summit (U2280, U2281) are tetraploid (n = 16). However, to the north all collections from the crest of the Front Range eastward are diploid. Clausen considered that plants from East Plum Creek, about 50 km. north of Pikes Peak near Larkspur, Colorado, are "reasonable topotypes" and reported that they are diploid (n = 8), but the ploidy of the type collection must still be regarded as uncertain. Study of the size of the pollen grains or stomatal guard cells might determine this definitely. Sedum borschii Clausen, endemic to Idaho and western Montana, was recently (1975) elevated from varietal status under S. leibergii. At metaphase I the lone plant studied here usually produced 16 bivalents and multivalents plus a variable number of univalents in different cells (Figure 17) and often had a laggard

or two and sometimes a bridge at anaphase I. Metaphase II plates had 17-23 elements, with 18 and 22 observed on the two plates in

one cell and 17-1-22 in another. This means that the somatic chromosome number must have been 40 and that the plant was pentaploid. Many microspore quartets included a small extra spore. Clausen (1975) also reported meiotic irregularities and/or differing and uncertain counts but "guessed" that the species is usually hexaploid, with n = 24. He considered vegetative reproduction to be important in the species but thought some functional seeds were produced. He also speculated about possible origin of the species as an allopolyploid hybrid between *S. leibergii* and *S. stenopetalum* and/or *S. lanceolatum*. The chromosome

number and behavior reported here are compatible with origin of S. borschii as a hybrid between octoploid S. stenopetalum (n = 32) and diploid S. leibergii (n = 8). The possibility that this species is a hybrid maintaining itself by asexual means needs further study.

Sedum debile S. Wats. is native chiefly to mountains of the Great Basin and adjacent areas to the north and east, from western Wyoming to Nevada and eastern Oregon. All 9 collections studied were diploid, n = 8, with one metacentric bivalent conspicuously larger than the others (Figure 8). The karyotype at meiotic metaphase appears constant in number and form. Clausen (1975) reported n = 8 for plants from three localities in the Grand Tetons.

Sedum divergens S. Wats., like the preceding, has decussate

leaves, but at maturity its carpels are spreading rather than erect. It occurs in the Cascade and Olympic Mountains from west central Oregon well north into British Columbia, with one or two isolated populations in the Klamath Mountains (Clausen, 1975). All 6 collections studied had n = 8, also with one bivalent larger than the others, but a bit less conspicuously so than in the preceding taxon (Figure 9). The meiotic chromosomes of S. divergens and S. debile appear very similar, and probably these two species are more closely related to each other than either is to any other species of Sedum. Clausen (1975) reported 2n = 16 for plants from a locality near Mount Baker, Washington, and another in the Wenatchee Mountains of central Washington, and Taylor and Mulligan (1968) reported n = 8 for plants from two localities in the Queen Charlotte Islands of British Columbia.

Sedum leibergii Britton is a small, often biennial species occurring chiefly on basalts of the Columbia Plateau. After flowering

it may die completely, or it may perennate by tiny lateral buds from the base of the inflorescence. Seven collections studied were all diploid (n = 8, Figure 10), and no prominent differences in size among the bivalents at meiosis were noted.

Sedum radiatum Watson and S. ciliosum Howell were previously classified as subspecies of the otherwise octoploid S. stenopetalum (Clausen, 1948). However, both are diploid (n = 8), and because of the differences in levels of ploidy and in some morphological characters, as well as their annual habit (though often perennating by lateral buds), Clausen (1975) now recog-

nizes S. radiatum as a separate species with three subspecies. Sedum radiatum subsp. radiatum (n = 8, Figure 11; 16 collections studied) occurs chiefly in the California Coast Ranges, with a few outlying populations in the southern Sierra Nevada and in the southern Klamath Mountains. To the north, in the central Klamath (Siskiyou) Mountains along the California-Oregon border, it is replaced by the newly described subsp. depauperatum Clausen (n = 8, Figure 13; 3 collections studied). Still farther north, subsp. *ciliosum* (Howell) Clausen (n = 8,Figure 12; 5 collections studied) is limited to southwestern Oregon in the northern Klamath Mountains and in the Coast Ranges. One larger metacentric bivalent is usually noted in all three subspecies (Figures 11-13), which have karyotypes similar to those of S. debile (Figure 8) and S. divergens (Figure 9). Sedum rupicolum G. N. Jones occurs in the northern Cascades and in the Wenatchee Mountains of central Washington, often on serpentine (Clausen, 1975). Both collections studied, one possibly from the type clone, were tetraploid (n = 16, Figure 14) and not distinguishable cytologically from tetraploid S. lanceolatum (Figure 5). This species does not seem much more distinct than certain other variants of S. lanceolatum, and it has previously been reduced to infraspecific status (Hitchcock & Cronquist, 1964). The type collection of Sedum stenopetalum was made in western Montana in 1806 by members of the Lewis and Clark expedition. Clausen (1948) reported that the type specimen also includes material of S. lanceolatum (which was later described accurately by Torrey in 1828), but Pursh's 1814 description of compressed subulate leaves and linear petals applies only to the former species. In 1840, W. J. Hooker recognized the existence

of two species, but he applied Pursh's name to the wrong element and redescribed S. stenopetalum as S. douglasii (Clausen, 1948). Unfortunately, Hooker's usage became standard for many years and was common in manuals and floras until only recently. Sedum stenopetalum (S. douglasii of many floras) occurs from southern British Columbia and western Montana to California. Its typical subspecies is consistently octoploid (n = 32, Figure 15; 32 collections). Some scattered populations, subsp. monanthum (Suksdorf) Clausen, are made up mostly or completely of plants with single-flowered inflorescences; moreover, the flowers are paler yellow. These also are octoploid (5 collections). Clausen (1975) reported that the species is octoploid, or approximately so, at four additional localities. Sedum oreganum Nuttall occurs in the Cascade Mountains and Coast Ranges from Oregon north to southern Alaska. It somewhat resembles S. divergens and was collected with that species at several places, e.g., Keechelus Lake (east of Snoqualmie Pass, Washington) and Tombstone Pass (Linn County, Oregon), but its leaves are flatter and not decussate, and its petals are connate basally. Plants of 15 collections made from southern British Columbia to the central Oregon coast all had n = 12 (Figure 16), as did plants from five other localities reported by Clausen (1975). This species is sometimes classed with Sedum subg. Gormania (Clausen, 1975), but all other species of that group have strictly n = 15 or a multiple of that number (Clausen & Uhl, 1944; Clausen, 1975; Uhl, unpublished). Thus, S. oreganum seems to be isolated cytologically, fitting into neither the Gormania group (x = 15) nor the lanceolatum group (x = 8), both of which are strictly euploid with different chromosome numbers. Clausen (1975) recognized two subspecies of Sedum oreganum. The larger subsp. oreganum occurs along the coast and in the Coast Ranges, and the slightly smaller subsp. tenue Clausen is endemic to the Cascade Mountains. Their chromosomes appear the same.

Polyploidy appears to be a very important isolating mechanism among these species. With only two apparent exceptions known, species of the *Sedum lanceolatum* group are always of different levels of ploidy where they occur together. Thus, *S. stenopetalum*

(n = 32) occurs with diploid S. lanceolatum (n = 8) at several places in the vicinity of Glacier National Park, Montana, (U398)

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& U399; U1197 & U1198; U1804 & U1805) and adjacent Waterton Lakes National Park, Alberta (U393 & U394), and doubtless elsewhere. It occurs with tetraploid S. lanceolatum (n = 16) in the Blue Mountains (U1189 & U1190) and Wallowa Mountains (U1565 & U1566) of northeastern Oregon, with hexaploid S. lanceolatum (n = 24) in southern British Columbia (U1812 & U1813), and in Jackson Hole, Wyoming (Clausen, 1975), and near the latter in north central Washington (U1956 & U1957). Sedum stenopetalum (n = 32, U1041, mostly one-flowered) occurs with S. rupicolum (n = 16, U1040) and at least near hexaploid S. lanceolatum (n = 24, U1814) in the Wenatchee Mountains of Washington, where Clausen (1975) has reported the presence also of diploid S. divergens (n = 8). Sedum stenopetalum subsp. monanthum (n = 32, U1212) occurs with S. radiatum subsp. depauperatum (n = 8, U1213) on Copper Butte in the Siskiyou Mountains of northern California. Hexaploid Sedum lanceolatum (n = 24, U1053) occurs with octoploid S. stenopetalum (n = 32) (Clausen, 1975) and with S. debile (n = 8, U1054) in the Grand Teton Mountains and/or Jackson Hole, Wyoming, near S. debile in Zion National Park, Utah (U1160 & U1159), and probably with S. debile in the Quinn Canyon (U1302) and Jarbridge Mountains (U1225) of Nevada. However, plants of S. debile from these last two locations died before counts could be obtained. Tetraploid S. lanceolatum

(n = 16, U1223) occurs with S. debile (not counted) in the East Humboldt Range of Nevada.

Two apparent exceptions are known to the rule that species of this group occurring together are of different levels of ploidy. In the Uinta Mountains of northern Utah diploid Sedum lanceolatum (n = 8, U1985-U1988) and S. debile (n = 8, U1990, U1991) both occur and flower at the same time. Unfortunately, plants of one or the other of the two species collected together there died before counts could be made. Clausen (1975) reported tetraploid S. lanceolatum (n = 16) from the Wenatchee Mountains in close proximity to S. rupicolum (n = 16), but my only count of S. lanceolatum from this area is hexaploid (n = 24, U1814).

The only aneuploids encountered were three probable poly-

somics and two plants with B-chromosomes (Figures 3, 4, & 6),

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all in Sedum lanceolatum. All clearly were casual variants, and aneuploidy has played no detectable role in evolution among these species. The only established variants found are polyploids, also in S. lanceolatum. In this species ploidy often appears to vary as an adjustment that favors its separate coexistence in proximity with other members of the group having a different level of ploidy. All other species, with the possible exception of S. borschii, are homogeneous in their ploidy.

At meiosis some polyploids exhibit probable multivalents and close secondary associations of bivalents, phenomena that suggest autopolyploidy. Compared to the diploids, the polyploids of Sedum lanceolatum show no greater resemblance to any other species, as would be expected if they were allopolyploids. Sedum stenopetalum is always octoploid, and one can only guess at its diploid progenitor(s). Clausen (1975) reported that natural hybrids occur between Sedum stenopetalum and S. lanceolatum in Jackson Hole, Wyoming, and in the Wenatchee Mountains of central Washington. However, in seven of eight morphological characters in his table (p. 281) the presumed hybrid closely resembles or transcends S. lanceolatum and shows no influence at all of S. stenopetalum. Sedum stenopetalum is always octoploid (n = 32), whereas S. lanceolatum is hexaploid (n = 24) in Jackson Hole and tetraploid and/or hexaploid in the Wenatchee Mountains. Thus, first-generation hybrids in Jackson Hole would be expected to be heptaploids with 2n = 56, and Clausen's hybrids are reported to have 2n = 50-59. He also reported and described a single natural hybrid between S. stenopetalum and S. borschii and mentioned possible hybrids of S. lanceolatum with S. rupicolum and S. divergens. The Klamath Mountains of southwestern Oregon and northwestern California are populated by octoploid plants of Sedum stenopetalum and five different diploids: S. lanceolatum (on mountain tops), all three subspecies of S. radiatum, and, according to Clausen (1975), two relictual populations of S. divergens. Apparently, none of the diploids occur together in this region. The principal distribution of S. divergens is contiguous to the north, and the ranges of the other two diploids, S. leibergii and

S. debile, are contiguous to the northeast and east, respectively.

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Sedum oreganum (n = 12) also occurs just north of this area, which is also a center of diversity for Sedum subg. Gormania (Clausen & Uhl, 1944). Whittaker (1960) pointed out that the Klamath region is geologically old, very diverse in climate and soils, and bears an old and very diverse flora. He considered it to be a "center" for forest floras of the West. It also may well have been the center of origin for the species considered here.

SUMMARY

Eight yellow-flowered species of Sedum of the western United States, S. lanceolatum, S. borschii, S. debile, S. divergens, S. leibergii, S. radiatum, S. rupicolum, and S. stenopetalum, all have a basic chromosome number of 8 and are believed to comprise a natural group. A ninth species, S. oreganum, is cytologically distinct with n = 12, and it seems taxonomically more isolated. Sedum lanceolatum includes widespread diploids, tetraploids and hexaploids. Sedum rupicolum is tetraploid, S. stenopetalum is octoploid, and S. borschii is often (always?) irregular at meiosis and may be a polyploid hybrid. All the remaining species are diploid. Polyploidy seems to be an important isolating mechanism between taxa when plants of two or more of these species occur together.

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APPENDIX I. COLLECTIONS STUDIED

Sedum borschii Clausen. (2n = 40, meiosis irregular.) Montana. MISSOULA COUNTY: Rattlesnake Valley, NE of Missoula (F. N. Rose) (C42-31).

Sedum debile S. Wats. (n = 8.)

Nevada. ELKO COUNTY: Lamoille Canyon, Ruby Mtns., 8000' (M. Williams) (U1072). NYE COUNTY: Pine Cr., E side of Mt. Jefferson, Toquima Range, 7800' (M. Williams) (U1561). Utah. CACHE COUNTY: Upper Logan Canyon, Wasatch Range, 13 mi. W of Garden City (U1058); Logan Canyon, 18 mi. NE of Logan (U1059). WASATCH COUNTY: Daniels Canyon, Wasatch Range, 11 mi. SE of Heber (U1063). SUMMIT COUNTY: Uinta Mtns., Stillwater Campground, 46 mi. NE of Kamas, 8600' (U1991); 9 mi. N of Mirror Lake, 9100' (U1990). WASHINGTON COUNTY: Hidden Canyon, Zion National Park, 5200' (U1159). Wyoming. TETON COUNTY: W side of Jenny Lake, Grand Teton Mtns. (U1054).

Sedum divergens S. Wats. (n = 8.)

Washington. CHELAN COUNTY: 5 mi. W of Merritt, 12 mi. E of Stevens Pass (U1815); KITTITAS COUNTY: Keechelus Lake, SE of Snoqualmie Pass (U1819); PIERCE COUNTY: White River, 28 mi. E of Enumclaw (U382); 0.25 mi. E of Cayuse Pass (U381). Oregon. HOOD RIVER COUNTY: east side of Mt. Hood (U1033). LINN COUNTY: Tombstone Pass, 4200' (U1183).

Sedum lanceolatum Torrey subsp. lanceolatum and subsp. subalpinum (Blankinship) Clausen. (n = 8.)

British Columbia. 7 mi. S of Merritt, 3500' (U1953); 9 mi. N of Princeton, n = 8 + 1B, 2300' (U1954); 18 mi. E of Princeton, 1200' (U1955); Crowsnest Pass, ¹/₄ mi. W of Alberta border (U391). Alberta. BANFF NATIONAL PARK:

Mt. Whitehorn, E of Lake Louise, 6750' (U1811); Mt. Norquay lift, Banff, 6900' (U1810). WATERTON LAKES NATIONAL PARK: 5 mi. N of Cameron Lake

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Sedum-Uhl

(U393). Oregon. JACKSON COUNTY: near summit, Mt. Ashland, Klamath Mtns., 7200' (U1971). California. SISKIYOU COUNTY: Scott Mt., 5700' (U1977). Montana. FLATHEAD COUNTY: 2 mi. NW of Logan Pass (U400); 1.8 mi. W of Marias Pass (U1806). GLACIER COUNTY: Rising Sun, Glacier National Park (U398, U1198); 3 mi. SW of East Glacier (U1804). TETON COUNTY: N Fork, Teton River, W of Choteau, 6000' (M. Williams) (U1567). CASCADE COUNTY: Little Belt Mtns., 2.5 mi. S of Neihart (U1803). BROADWATER COUNTY: 22 mi. E of Townsend, Big Belt Mtns. (U1801). GALLATIN COUNTY: Gallatin River, 27 mi. S of Bozeman (U1049). Wyoming. YELLOWSTONE NATIONAL PARK: 9.7 mi. W of Tower Junction (U1794); 1.6 mi. SE of Tower Junction (U2172); decomposing geyserite near Giantess Geyser, 350 meters N of Old Faithful (U1052). WASHAKIE COUNTY: 16 mi. NE of Tensleep, Big Horn Range (U1774). NATRONA COUNTY: Hells Half Acre, 4 mi. W of Powder River (U1195). ALBANY COUNTY: Vedauwoo Glen, 18 mi. SE of Laramie, Sherman Mtns. (U1075, U1735); Tree-in-Rock, 20 mi. SE of Laramie (U1998). LARAMIE COUNTY: 22 mi. W of Cheyenne, Sherman Mtns. (U1736). Utah. SUMMIT COUNTY: 6 mi. N of Mirror Lake, Uinta Mtns. (U1988); Bald Mountain Pass, 29 mi. E of Kamas, 10650' (U1986); 22 mi. E of Kamas (U1985). DUCHESNE COUNTY: Mirror Lake, Uinta Mtns., 9950' (U1987). Colorado. LARIMER COUNTY: 4.5 mi. NW Virginia Dale, Sherman Mtns., 7700' (U2196); Rawah Wild Area, 10,800' (D. D. Koob) (U532, U687); Alpine tundra, Fall River Pass, 11,800' (U1067); Fall River Road, 10,000' (U2208A, n = 9 + 1; U2208B, U2208C, n = 8); Trail Ridge, 4.4 & 6.7 mi. SE of Fall River Pass, 12,125 & 11,800' (U2210, U2211); Horseshoe Park, (U2207); 4.5 mi. W of Estes Park (U2212); W side of Estes Park (U1070); E side of Estes Park (U2206); 5 mi. S of Estes Park (U2205); 6 mi. SE of Estes Park (U2213); 2.7 mi. N of Meeker Park (U2204); Big Thompson Canyon, 15 mi. W of Loveland (U1071); 1.5 mi. NW Pinewood Springs (U2214). GRAND COUNTY: 6.3 mi. SW Milner Pass (U1065*). BOULDER COUNTY: 5 mi. SE Pinewood Springs (U2215); 2.5 mi. S of Meeker Park (U2203); 2.5 mi. NW of Raymond, 9000' (U2202); 6 mi. N of Ward, 9300' (U2201); 0.5 mi. N of Ward (U2200); 7 mi. N of Nederland, 8600' (U2199); 4 mi. W of Boulder (U2197); Chautauqua, Boulder (U1340); Eldorado Springs (U1339). CLEAR CREEK COUNTY: Idaho Springs, 7700' (U2228); 5 mi. SW of Idaho Springs (U1334). JEFFERSON COUNTY: 13 mi. W of Denver, 7500' (U2232); Bergen Park (NY Bot. Gard.) (C46-39); 3 mi. SW Morrison (U1588); 1 mi. SW Conifer Junction (U1589); 1 mi. NE of Silver Springs (U1590); 1.6 mi. S of Buffalo Creek (C. H. Uhl, Jr.) (U2279). PARK COUNTY: Kenosha Pass, 10,000' (U1591). GUNNISON COUNTY: 7.5 mi. NE of Almont, 8600' (U2241). CUSTER COUNTY: Wet Mtns., 9 mi. NW of Fairview (U1603); Fairview, 9300' (U1602); 5.5 mi. NW San Isabel (U1601); San Isabel, n = 8 + 1 (U1600). PUEBLO COUNTY: 4 mi. NW Rye (U1599). MINERAL COUNTY: 4.5 mi. W of Wolf Creek Pass, San Juan Mtns. (U1595). HUERFANO COUNTY: 1.5 mi. E of La Veta Pass, Culebra Range, 9200' (U1596).

Sedum lanceolatum Torrey subsp. lanceolatum and subsp. subalpinum (Blankinship) Clausen. (n = 16.)

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Washington. PIERCE COUNTY: Castle Mt., NE of Mt. Rainier, 6500' (M. Williams) (U1254). Oregon. GRANT COUNTY: serpentine 1 mi. E of Dixie Pass, Blue Mtns. (U1190). WALLOWA COUNTY: N slope, Joseph Mt., Wallowa Mtns., 7000' (M. Williams) (U1562). Nevada. ELKO COUNTY: near Angel Lake, East Humboldt Range (M. Williams) (U1223). Montana. MEAGHER-CASCADE COUNTY LINE: Kings Hill Pass, Little Belt Mtns., 7400' (U1802). PARK COUNTY: 0.4 mi. W of Silvergate (U1791); Colter Pass, 8060' (U1790). CARBON COUNTY: Rock Creek Observation Point, 21 mi. SW Red Lodge (U1785*); 13 mi. SW of Red Lodge (U1784); 4 mi. SW of Red Lodge (U1783). Wyoming. YELLOW-STONE NATIONAL PARK: 8 mi. E of Tower Junction (U1793); 20 mi. E of Tower Junction (U1792); 22 mi. E of Tower Junction (U2171); below Virginia Cascades (U1800); spur road to Mt. Washburn, 8200' (U1051*); Canyon Junction (U2184); Hayden Valley, 9 mi. S of Canyon Junction (U2187); 1 mi. N of Lake Junction (U2188); spur road to Natural Bridge (U403); 4.25 mi. SW of Lake Junction (U2189); 10 mi. NE West Thumb (U2190); 3.2 mi. NW of West Thumb, 8300' (U2191). PARK COUNTY: Clarks Fork, 9.75 mi. SE of Cooke City, Mont. (U1789*); 1 mi. W of Beartooth Lake (U1788*); alpine tundra at Beartooth Pass, 10,950' (U1787); 3.5 mi. N of Beartooth Pass, in alpine tundra (U1786). BIG HORN COUNTY: W side Medicine Mt., Big Horn Range, 29 mi. E of Lovell (U1782*); near Bald Mt. Campground, 37 mi. E of Lovell (U1780); 15 mi. W of Burgess Junction, Big Horn Range (U1779*); 3.75 mi. above Shell Falls (U1775); 1 mi. above Shell Falls (U405). SHERIDAN COUNTY: N Tongue River, 10 mi. W of Burgess Junction (U1778); 0.25 mi. W of Burgess Junction (U2170); 0.5 mi. N of Granite Pass, 8900' (U1776); 7.75 mi. E of Burgess Junction (U2169); 13 mi. W of Dayton (U2168). WASHAKIE COUNTY: Meadowlark Lake, Big Horn Range (U1773). JOHNSON COUNTY: alpine tundra at Powder River Pass, Big Horn Range, 9670' (U1772); 3 mi. E of Powder River Pass (U1771); 25 mi. SW of Buffalo (U1770); 16 mi. W of Buffalo, Big Horn Range (U1768). CARBON COUNTY: Arlington, in gravelly roadside (U1995); 6.75 mi. N of Riverside (U1727); 16.5 mi. SE of Saratoga (U1728); above Silver Lake, Snowy Range (U1729); Libby Flats, Snowy Range, 10,800' (U1730). ALBANY COUNTY: 1.25 mi. W of Centennial (U1732); 12 mi. SE of Laramie (U1996); 6 mi. E of Laramie, Sherman Mtns. (U1733); 9.5 mi. E of Laramie (U1734); 2 mi. SE of Tie Siding (U2194); 4.25 mi. SE of Tie Siding (U2195). South Dakota. PENNINGTON COUNTY: 1.5 mi. W of Mt. Rushmore (U1764). CUSTER COUNTY: S of Hood Tunnel (U1765); Needles Eye (U1766); 0.5 mi. E of Stockade Lake (U1767). Utah. SAN JUAN COUNTY: Pine Ridge, 3.7 mi. E of La Sal, La Sal Mtns. (U1614). Arizona. APACHE COUNTY: Tsaile Creek, 15.6 mi. N of Wheatfield Lake on Roof Butte Road, Chuska Mtns., 8000' (C. H. Uhl, Jr.) (U2285). Colorado. GRAND COUNTY: Hot Sulphur Springs (U1064); 9.5 mi. NW of Granby (U1722); Milner Pass, 10,760' (U1066); Big Meadows, 4 mi. N of Grand Lake (U2227); Cascade Falls, 4 mi. NE of Grand Lake (U2226); E side Grand Lake, 8400' (U2220); N tip, Granby Lake (U2221); SW corner, Granby Lake (U2222); S side Granby Lake (U2224); 0.5 mi. W of Monarch Lake (U2223); 1 mi. N of Granby (U1720*); 0.5 mi. N of Fraser (U1719); 3.5 mi. N of Berthoud Pass (U1717); Berthoud Pass, 11,320' (U1716). CLEAR CREEK COUNTY: 7.5 mi. W of Empire (U1715); 4.25 mi. W of Empire (U1714); Loveland Pass, in tundra, 12,000' (U1333); W side of Dillon Reser-

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voir, 2 mi. N of Frisco (U1713); 1.75 mi. S of Frisco, 9300' (U2233); 5.75 mi. SE of Frisco (U2234); 1.75 mi. SE of Vail Pass, 10,300' (U2276); 1 mi. N of Climax, 11,250' (U1330). PITKIN COUNTY: 10 mi. W of Independence Pass, Sawatch Range (U1611). EAGLE COUNTY: Tennessee Pass, 10 mi. N of Leadville, 10,425' (U1707). LAKE COUNTY: 7.5 mi. N of Leadville (U1706); 5 mi. SW of Climax (U1705); 13 mi. W of Twin Lakes, Sawatch Range (U1606); 7 mi. W of Twin Lakes, 10,000' (U1605); 1.5 mi. W of Twin Lakes (U1604). PARK COUNTY: 2 mi. S of Alma (U2236). MONTROSE COUNTY: Campground and Oragon Point, Black Canyon of the Gunnison National Monument (U1697, U2284). GUNNISON COUNTY: S side of Taylor Reservoir (U2240); 8 mi. W of Cottonwood Pass, Sawatch Range, 10,400' (U2239); Monarch Pass, 11,350' (U1328). CHAFFEE COUNTY: 4 mi. N of Monarch Pass, 10,000' (C. H. Uhl, Jr.) (U2282). TELLER COUNTY: Middle Beaver Creek, 0.5 & 3.3 mi. N of Clyde Campground, 7 & 4.5 mi. S of Pikes Peak summit, 9550' & 10,900' (C. H. Uhl, Jr.) (U2281, U2280). SAN MIGUEL COUNTY: 4.25 mi. N of Lizard Head Pass, La Plata Mtns., 0.5 mi. S of Ophir (U1696). OURAY COUNTY: Ouray (U1325); 1.5 mi. S of Ouray (U1324). SAN JUAN COUNTY: Red Mountain Pass, 11,090' (U1322); 16 mi. S of Silverton (U1318). HINSDALE COUNTY: 2 mi. S of Lake City (U1694). MINERAL COUNTY: North Creede, 9100' (U1592); 7 mi. NE of Wolf Creek Pass (U1594). HUERFANO COUNTY: Blue Lakes, above Cucharas Pass, Culebra Range, 10,000' (U1597). New Mexico. TAOS COUNTY: 2.7 mi. E of Questa (U1139). COLFAX COUNTY: 2.5 mi. E of Red River Pass, Sangre de Cristo Range (U1135).

Sedum lanceolatum Torrey subsp. lanceolatum. (n = 24.)
British Columbia. W end of Yellow Lake, 17 mi. SW Penticton (U1813).
Washington. CLALLAM COUNTY: Olympic Mtns. (W. C. Muenscher 813).

OKANOGAN COUNTY: near dam, Conconully Lake (U1957). CHELAN COUNTY: Mission Ridge Ski Area, 11 mi. SE of Wenatchee (U1814). Idaho. BONNER COUNTY: Cabinet Gorge Dam (H. W. Blaser) (U1817). BONNEVILLE COUNTY: 10 mi. N of Swan Valley, Big Hole Mtns. (U1192). California. ALPINE COUNTY: Carson Pass, 8600' (U1163); above Blue Lakes, S of Carson Pass (P. C. Hutchison 2149) (U985). MONO COUNTY: 1 mi.N of Tioga Pass (U974). Nevada. HUMBOLDT COUNTY: E slope, Granite Peak, Santa Rosa Mtns., 8500' (R. Ornduff) (U1010). ELKO COUNTY: along Jarbridge River, Jarbridge Mtns. (M. Williams) (U1225). LANDER COUNTY: S of Austin Summit, Toiyabe Mtns. (U1117, U1161). NYE COUNTY: above Cherry Creek Summit, Quinn Canyon Range (M. Williams) (U1362). Utah. KANE COUNTY: 0.5 mi. N of E entrance, Zion National Park (U1160). Montana. GALLATIN COUNTY: West Yellowstone (U2177). Wyoming. YELLOWSTONE NATIONAL PARK: 4 mi. E of West Entrance (U2176); 5.75 mi. W of Madison Junction (U2175); 2.25 mi. W of Madison Junction (U2178); rotting travertine at Mammoth Hot Springs (U1050); 10 mi. S of Mammoth Hot Springs (U2183); 6.5 mi. N of Norris Junction at Beaver Ponds (U2182); 0.75 mi. W of Gibbon Falls (U2181); 2 mi. E of Madison

Junction (A. Witztum) (U1196); Firehole Canyon (U2179); S side, Firehole Lake (U1795); 1.4 mi. S of Firehole Lake (U2173); observation point, Old

Faithful (U1796*). PARK COUNTY: Pahaska (J. M Kingsbury) (U432). TETON COUNTY: W side of Jenny Lake (U1053); 2 mi. S of Jenny Lake, in sagebrush (U2192); 1.5 mi. W of Togwotee Pass, Wind River Range, 9300' (U1194). LINCOLN COUNTY: 7.5 mi. NE of Alpine (U1055). Colorado. EAGLE COUNTY: 8 mi. S of Gilman (U1708); 8.7 mi. SE of Vail, 9200' (U2217). SUMMIT COUNTY: 2.25 mi. SE of Vail Pass, Gore Range (U1710, U2216); 4.75 mi. SE of Vail Pass, 9900' (U1711); 5.5 mi. SW of Frisco (U1331); 4.75 mi. SW of Frisco (U1712).

Sedum lanceolatum Torrey subsp. nesioticum (G. N. Jones) Clausen. (n = 24.) British Columbia. Cattle Point, Victoria (U385). Washington. WHATCOM COUNTY: Lummi I. (W. C. Muenscher 7931).

Sedum leibergii Britton. (n = 8.)

Oregon. HOOD RIVER COUNTY: 1 mi. E of Hood River (*U1035*). WASCO COUNTY: 2.5 mi. W of Celilo (*U1037*); Cow Canyon, 2.5 mi. N of Willowdale (*U1961*). WHEELER COUNTY: Mitchell (*U1185*); Mountain Creek, 17.5 mi. E of Mitchell (*U1186*); 20 mi. E of Mitchell, 3450' (*U1187*). GRANT COUNTY: Rock Creek, 7.75 mi. W of Dayville (*U1188**).

Sedum oreganum Nuttall subsp. oreganum. (n = 12.)
British Columbia. Horseshoe Bay, 20 mi. N of Vancouver (UC62.306).
Washington. WHATCOM COUNTY: Lummi I. (W. C. Muenscher 7923); Ruby Creek (W. C. Muenscher 7929). PACIFIC COUNTY: N side of Cape Disappointment, S of Ilwaco (U1027). WAHKIAKUM COUNTY: 4 mi. E of Cathlamet (U1029). Oregon. TILLAMOOK COUNTY: sea bluff, 4 mi. N of Nehalem (U379). LANE COUNTY: sea cliffs, 6 mi. S of Yachats (U378).

Sedum oreganum Nuttall subsp. tenue Clausen. (n = 12.)
Washington. PIERCE COUNTY: White River, 28 mi. E of Enumclaw (U383);
SW entrance to Mt. Rainier National Park (U1178). KITTITAS COUNTY: Keechelus Lake, 7 mi. E of Snoqualmie Pass (U1818). LEWIS COUNTY: Cowlitz River at Nesika (U380). Oregon. MULTNOMAH COUNTY: Sandy River, 2 mi. S of Troutdale (R. Bacigalupi et al.) (U978); Latourelle Falls (R. Bacigalupi et al.) (U980); Sheppards Dell (R. Bacigalupi et al.) (U982). LINN COUNTY: Tombstone Pass, 4200' (U1181).

Sedum radiatum S. Wats. subsp. radiatum. (n = 8.)

California. HUMBOLDT COUNTY: Klamath River, 4 mi. N of Orleans (U936). MENDOCINO COUNTY: 3 mi. SE of Cummings (M. Kimnach 56) (U371); 5.25 mi. SE of Cummings (U929); 3 mi. S of Longvale (M. Kimnach) (UC53.493). LAKE COUNTY: 6 mi. SE of Lakeport (R. Moran 3385). SONOMA COUNTY: N of Occidental (H. Roberts) (UC52.496). NAPA COUNTY: 6 mi. NE of Calistoga (M. A. Nobs) (M3245). MARIN COUNTY: Walker Creek Bridge, 1.5 mi. S of Tomales (W. Roderick) (U1167); Nicasio Creek, 3 mi. E of Pt. Reyes Station (U365); 1 mi. W of Lagunitas, 200' (U364); Upper Lucas Valley, 5 mi. SE of Nicasio (U362). SANTA CRUZ COUNTY: 3.5 mi. NW of Boulder Creek (U924).

SAN BENITO-MONTEREY COUNTY LINE: (TOPOTYPE), near summit of Fremont Peak, 3050' (U903). TUOLUMNE COUNTY: S Fork, Tuolumne River at Cliff

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Sedum-Uhl

House (U366). MARIPOSA COUNTY: Pohono Trail, above Wawona Tunnel, Yosemite National Park (U367). FRESNO COUNTY: Stevenson Creek, below Shaver Lake Dam, 5300' (U909).

Sedum radiatum S. Wats. subsp. depauperatum Clausen. (n = 8.)
Oregon. JACKSON COUNTY: on serpentine (?) along Applegate River, 0.25 mi. S of Copper, 1750' (U1968); 10 mi. SE McKee Bridge (P. C. Hutchison 962 = UC62.1115). California. SISKIYOU COUNTY: on serpentine (?), Copper Butte, N of Seiad Valley, 5200' (M. Williams) (U1213).

Sedum radiatum S. Wats. subsp. ciliosum (Howell) Clausen. (n = 8.) Oregon. JOSEPHINE COUNTY: Grave Creek Bridge over Rogue River (U950); Rogue River at Hellgate Bridge, 6 mi. S of Galice (U947). DOUGLAS COUNTY: 6.5 mi. S of Tiller (P. C. Hutchison 2616) (UC62.1123). JACKSON COUNTY: Rogue River at Shady Cove (U944); W of McLeod (U1023).

Sedum rupicolum G. N. Jones. (n = 16.)

Washington. CHELAN COUNTY: (TOPOTYPE), on serpentine along Peshastin Creek, 6.6 mi. N of Swauk Pass, Wenatchee Mtns. (U1040*). Cultivated. Possibly from type clone (see Clausen, 1975) (C388).

Sedum stenopetalum Pursh subsp. stenopetalum. (n = 32.)

British Columbia. W end of Yellow Lake, 17 mi. SW of Penticton (U1812). Alberta. WATERTON LAKES NATIONAL PARK: 5 mi. N of Cameron Lake (U394); Cameron Falls (U392). Washington. WHATCOM COUNTY: Harts Pass (W. C. Muenscher) (C131). OKANOGAN COUNTY: 3 mi. NW of Conconully (U1956); 1 mi. SE of Desautel Pass (U390). KITTITAS COUNTY: Swauk Creek, 9 mi. NE of Teanaway, Wenatchee Mtns. (U1039). PEND OREILLE COUNTY: 16 mi. SW of Newport (U1043). Oregon. COLUMBIA COUNTY: 1 mi. N of St. Helens (M. Kimnach) (UC52.1294). CROOK COUNTY: Marks Creek, 22 mi. E of Prineville (U1184). WHEELER COUNTY: 1.75 mi. E of Ochoco Pass (J. Weiler et al.) (U983). GRANT COUNTY: 5 mi. S of Long Creek, 4000' (M. Williams) (U1252); 1 mi. E of Dixie Pass, Blue Mtns., 5100' (U1189). BAKER COUNTY: 1 mi. E of Blue Mountain Pass (U1191). WALLOWA COUNTY: N slope, Joseph Mt., Wallowa Mtns. (M. Williams) (U1565). California. MODOC COUNTY: Cedar Pass, Warner Mtns., 6200' (W. Roderick) (U966); 2 mi. NE of Cedar Pass (M. Williams) (U1119). Idaho. BOUNDARY COUNTY: below Moyie Falls, 9 mi. E of Bonners Ferry (U1045). BONNER COUNTY: 2.25 mi. W of Laclede (U1044). KOOTENAI COUNTY: N shore Lake Coeur d'Alene (U1820); East Point, Lake Coeur d'Alene, near Harrison (G. Bowne) (U409). Montana. LINCOLN COUNTY: Kootenai River, 5 mi. SE of Troy (U1046); 3 mi. N of Olney (U1809). FLATHEAD COUNTY: McGregor Lake, 31 mi. W of Kalispell (U1047); Somers (U1048); Flathead River, 0.5 mi. E of West Glacier (U1808); 16 mi. SE of West Glacier (U1807). GLACIER NATIONAL PARK: Many Glacier (U396); Rising Sun (U399, U1197). MISSOULA COUNTY: Marshall Creek, 4.5 mi. NE of Missoula (U401); Clark Fork, 22 mi. SE of Missoula



Sedum stenopetalum Pursh subsp. monanthum (Suksdorf) Clausen. (n = 32.) Washington. CHELAN COUNTY: Peshastin Creek, 6.5 mi. N of Swauk Pass (U1041, mostly one-flowered). Oregon. HOOD RIVER COUNTY: near Bottle Prairie, E of Mt. Hood (U1031). JACKSON COUNTY: 1 mi. S of Siskiyou Summit (U942). California. SISKIYOU COUNTY: Copper Butte, N of Seiad Valley, 5200' (M. Williams) (U1212). GLENN COUNTY: 6.5 mi. S of Mendocino Pass, 6400' (M. Williams) (U1248).

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